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A REVIEW OF THE TAXONOMIC STATUS OF *HACKELIA VENUSTA* (BORAGINACEAE)

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ABSTRACT. Morphological variables were analyzed using principal components and discriminant analyses to determine patterns of relationships among populations of *Hackelia venusta,* a narrow endemic, and *H. diffusa* var. *arida,* a relatively common species. The results of the analyses indicate that *H. venusta,* as currently circumscribed, consists of two discordant taxa with the population from the type locality at a low elevation clearly distinct from high elevation populations that have been assigned to this species. The high elevation populations represent an undescribed taxon. No affinities with either the low elevation *H. venusta* or the high elevation undescribed taxon were found to exist with populations of *H. diffusa* var. *arida.* Both *H. venusta* and the undescribed high elevation taxon are very narrow endemics and would benefit from well-developed conservation strategies and subsequent management.

Key Words: *Hackelia,* taxonomy, rare species

Hackelia venusta (Piper) St. John, showy stickseed, is a narrow endemic species of the Boraginaceae currently known only from Chelan County, Washington. As described by Gentry and Carr (1976), the species is a moderately stout perennial, 2–4 dm tall, often with numerous, erect to ascending stems from a rather slender taproot. It has large, white, showy flowers. The nutlets are 3–4.5 mm long, with 8–14 intramarginal prickles. The marginal prickles are fused for up to ½ their length, forming a flange ca. 1 mm wide. It is found on steep, rocky slopes covered with granitic scree.

The species was first described by Piper (1924) in the genus *Lappula* and was later transferred to *Hackelia* by St. John (1929). The original description given by Piper was based on a 1920 collection made by J.C. Otis (*895,* US) at a site about seven miles northwest of Leavenworth in Tumwater Canyon at an elevation of 488 meters. Piper described *H. venusta* as having a white corolla about 2 cm broad. In 1947, a specimen (*Long 14,* WS) was collected about 16 km south, southwest of the Otis collection in the Alpine Lakes Wilderness, Chelan County, at an elevation of 2030 meters. Subsequently, researchers (Carr 1974; Gentry and Carr 1976; Hitchcock et al. 1959) included this alpine collection in their circumscription of the species and noted that flowers are white or sometimes washed with blue. Since that time, three additional alpine populations assumed to be *H. venusta* have been located, one from an area near the Otis collection (*Harrod 238,* Leavenworth Ranger District Herbarium), one from Asgaard Pass (plants have not been relocated since 1995, Harrod unpubl. data) and the other from Cashmere Mountain, all above 2000 meters within the Alpine Lakes Wilderness area.

Some recent workers have suggested that the high elevation populations may be taxonomically distinct from the Tumwater Canyon *Hackelia venusta* (Gamon 1988; Loyal A. Mehrhoff, USFWS, Portland, OR, and Kathleen Robson, Robson Botanical Consultants, Vancouver, WA, pers. com.). The purpose of this study was to evaluate the relationship of these populations in order to achieve a better understanding of the taxonomic status of *H. venusta.* Because of the possibility of some allopatric introgression between *H. venusta* (*sensu stricto*) and populations of *H. diffusa* (Doug. ex Lehmann) Johnston var. *arida* (Piper) Carr in the lower end of Tumwater Canyon and several coulees north of Leavenworth (Carr 1974; Gentry and Carr 1976), a number of populations of the *H. diffusa* var. *arida* were included in the study.

MATERIALS AND METHODS

Study sites. Data were collected from ten populations in Washington shown on the map in Figure 1. Collection sites for *Hackelia venusta* (*sensu lato*) were located on the Wenatchee National Forest in Tumwater Canyon (TC), 9.6 km west of Leavenworth, 488 meters; Crystal Creek (CC), 19.0 km southwest of Leavenworth, 2030 meters; and on Cashmere Mountain (CM), 16.0 km southwest of Leavenworth, 2073 meters. Collection sites for *Hackelia diffusa* var. *arida* were located on the Wenatchee National Forest in Tumwater Canyon (TW), 1.6 km west of Leavenworth, 400 meters; Derby Canyon (DE), 11.3 km southeast of

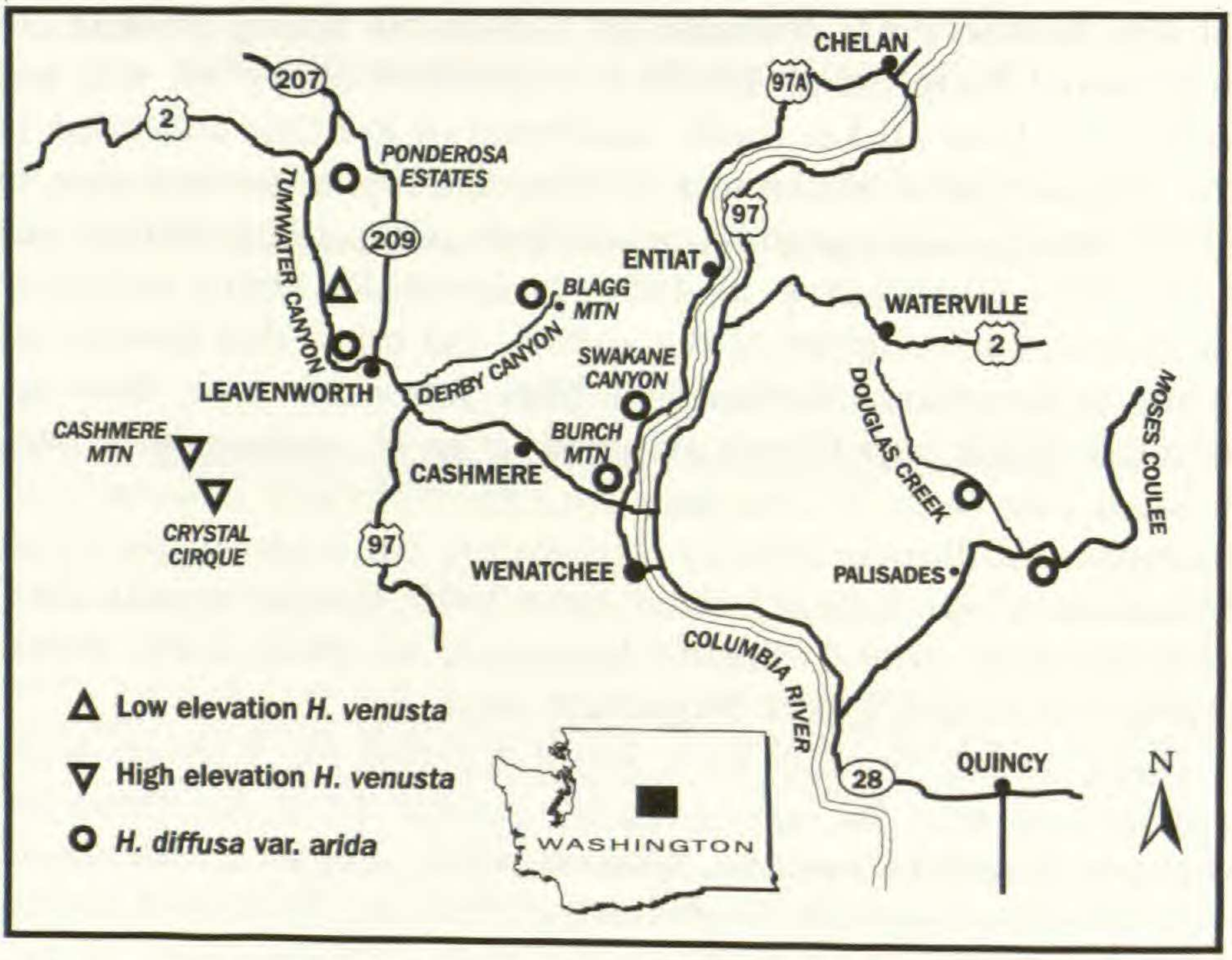

Figure 1. Locations of the populations of *Hackelia* examined in this study.

Leavenworth, 730 meters; Burch Mountain (BM), 4.8 km northwest of Wenatchee, 400 meters; Swakane Canyon (SC), 19.3 km northeast of Wenatchee, 1188 meters; and on the Ponderosa Estates Special Interest area (PE), 17.7 km north of Leavenworth, 670 meters. Two sites were located on Bureau of Land Management land; in Moses Coulee (MC), 24.0 km north of Quincy, 152 meters; and Douglas Creek (DC), 26.0 km north of Quincy, 140 meters.

Voucher specimens from each population of *Hackelia diffusa* var. *arida* (TW: *Malmquist 01, 02*; DE: *Malmquist 05, 06, 07*; BM: *Harrod 411*; SC: *Harrod 413*; PE: *Malmquist 08*; MC: *Malmquist 03, 04*; DC: *Harrod 349*) and from each of the Crystal Creek (*Carr et al. 3364*), Cashmere Mountain (*Kuhlmann 01*; *Benson 01*) and Tumwater Canyon (*Harrod 293*) populations of the putative *H. venusta* are deposited in the Leavenworth Ranger District Herbarium in Leavenworth. Voucher specimens from all three populations of the putative *H. venusta* (*sensu lato*) are deposited in WTU (TC: *Harrod 410*; CC: *Carr et al. 3364*; CM: *Benson 02*).

Morphological characters. Characters selected generally follow those used by Gentry and Carr (1976). Nineteen morphological characters from three categories were scored for statistical analysis (vegetative, floral, and fruit) and an additional 11 qualitative characters were recorded (Table 1). At each site, 25 plants were chosen randomly, numbered, and tagged. The Cashmere Mountain site, however, supports a small population and only 14 plants were selected. From each plant, one radial (basal) leaf and two cauline leaves, one from the lower one-third and one from the upper one-third of the stem, were chosen randomly for measurement. Three flowers and three fruits were chosen randomly and measured on each plant.

Statistical analyses. Both principal components and discriminant analyses were performed on the quantitative morphological data (SYSTAT 1997, SPSS Inc., Chicago, IL). Principal components analysis (PCA) was used to show natural groupings among each sampling unit or operational taxonomic unit (population). PCA is a method of partitioning a resemblance matrix into a set of perpendicular components (Ludwig and Reynolds 1988). Each component or axis has a corresponding eigenvalue which is the variance accounted for by that axis. The eigenvalues of the matrix are separated in descending order of magnitude so that each PCA component represents successively lesser amounts of variation (Ludwig and Reynolds 1988). The first component is the linear combination of variables accounting for more variance in the data than any other possible combination. The second component is the linear combination of the remaining variance after the first component is accounted for, the third component is the best linear combination after the first and second components have been accounted for, and so on. The data for the PCA involved the entire data set of a 238 $\times$ 19 character matrix (Table 1).

Discriminant analysis was used to establish the nonarbitrariness of group assignments. This analysis places each case within the group (population) with which it shares discriminating characters (Anderson and Taylor 1983). Unlike PCA, discriminant analysis is biased in that it positions cases within the ordination based on discriminating characters to achieve maximum separation of previously defined groups. The case distributions were plotted by two discriminant functions that separated the assigned groups to

Table 1. Morphological characters used in the taximetric analysis of *Hackelia venusta* and *H. diffusa* var. *arida*. All measurements in mm unless otherwise noted.

Vegetative	Floral	Fruit
Plant height (dm)	Pedicel length	Nutlet shape (descriptive)
Radial leaf length	Calyx length	Nutlet surface (descriptive)
Radial leaf width	Calyx shape (descriptive)	Nutlet length
Radial leaf petiole length	Limb width	Number of intramarginal prickles
Radial leaf shape (descriptive)	Corolla color (descriptive)	Flange width
Radial leaf surface (descriptive)	Anther length	Distinct prickle length
Lower cauline leaf length	Fornice color (descriptive)	Fraction connate
Lower cauline leaf width	Fornice appendage height	
Lower cauline leaf shape (descriptive)	Fornice protuberance length	
Lower cauline leaf surface (descriptive)		
Upper cauline leaf length		
Upper cauline leaf width		
Upper cauline leaf shape (descriptive)		
Upper cauline leaf surface (descriptive)		

Table 2. Means and standard deviation (in parentheses) of characters used in the present study. Measurements are given in mm, except height which is in dm. [1]Abbreviations of the quantitative characters listed in Table 1.

Character[1]	Blue-flowered *Hackelia venusta* n = 2	White-flowered *Hackelia venusta* n = 1	*Hackelia diffusa* var. *arida* n = 7
Floral			
Ped	3.7 (1.42)	6.3 (1.88)	4.4 (1.84)
Clx	3.0 (0.43)	3.8 (0.54)	2.4 (0.50)
LimWid	4.2 (0.72)	7.4 (1.84)	4.3 (0.98)
Anth	0.9 (0.13)	1.0 (0.15)	1.0 (0.52)
For/Ap	1.0 (0.14)	1.3 (0.20)	0.6 (0.20)
For/Pr	0.8 (0.19)	1.5 (0.31)	0.7 (0.32)
Fruit			
NutL	5.6 (0.85)	6.4 (0.88)	6.2 (1.14)
#InPr	10.2 (2.86)	11.4 (2.92)	10.1 (3.93)
FlW	1.8 (0.34)	1.9 (0.38)	1.5 (0.52)
DPL	1.2 (0.25)	1.1 (0.76)	1.0 (0.53)
FrCon	0.4 (0.11)	0.5 (0.08)	0.3 (0.12)
Vegetative			
Height (dm)	1.4 (0.35)	2.7 (6.74)	5.1 (1.40)
RL:L	56.9 (16.36)	48.9 (11.6)	98.6 (41.0)
RL:W	14.4 (4.60)	11.3 (4.08)	8.8 (4.00)
RL:Pet	21.9 (9.50)	32.2 (10.4)	63.3 (26.4)
CLL:L	28.8 (6.64)	37.3 (11.0)	83.2 (23.3)
CLL:W	9.2 (2.85)	7.4 (2.00)	4.5 (1.62)
CLU:L	15.0 (5.67)	20.1 (6.50)	31.5 (13.3)
CLU:W	6.5 (2.26)	6.6 (2.40)	3.7 (1.60)

the greatest ability. Again, the data for this analysis involved the same 238 × 19 character matrix used in the PCA.

Qualitative characters were not subjected to statistical analyses, but are used for further discussion and description.

RESULTS

The means and standard deviations for the quantitative characters are presented in Table 2 for each putative taxon. The Crystal Creek and Cashmere Mountain populations, which were blue-flowered, consistently had smaller floral measurements than the white-flowered *Hackelia venusta* of Tumwater Canyon. However, there were no consistent differences between these populations and the *H. diffusa* var. *arida* populations; there is considerable variability in floral size among populations of this latter, complex taxon. Fruit characteristics tended to be similar among all populations. The Tumwater Canyon *H. venusta* were taller in stature than the Crystal Creek and Cashmere Mountain populations, but similar to all populations of *H. diffusa* var. *arida* that were analyzed. Leaf characteristics were variable, with the Tumwater Canyon *H. venusta* having the shortest radial leaves but intermediate in leaf length for the upper and lower cauline leaves. The Crystal Creek and Cashmere Mountain populations had the widest radial and lower cauline leaves.

Radial leaf and nutlet measurements were missing from a number of cases at the conclusion of the study. These characters were dropped from both the principal components and discriminant analyses since the program would ignore those cases with missing data.

Principal components analysis. Each plant (case) was assigned a symbol representing its membership in the populations (OTUs) sampled. Natural groups were developed among the 238 cases by plotting the principal component scores. Of the 11 components that accounted for all the variance, the first three accounted for 68.0% (38.5%, 18.3%, and 11.2%, respectively). The groups (populations) are arranged in the ordination shown in Figure 2 based on the first two principal components. An isolated group was formed by 22 cases from the Tumwater Canyon population of *Hackelia venusta.* Two of the remaining cases were marginally associated with the *H. diffusa* var. *arida* complex and the third tended to be marginally associated with cases belonging to the Cashmere Mountain and Crystal Creek populations.

The Cashmere Mountain and Crystal Creek populations also formed a distinct group (Figure 2) although there appeared to be some overlap with cases from the Ponderosa Estates and Moses Coulee populations of *Hackelia diffusa* var. *arida.* One case from the Cashmere Mountain population was associated with Swakane Canyon, Birch Mountain, and Tumwater Canyon populations of *H. diffusa* var. *arida.*

Finally, there was considerable overlap in the *Hackelia diffusa* var. *arida* cases with no distinct groups (Figure 2). However, there is some separation based on populations; the Swakane Canyon, for example, is separated from Ponderosa Estates and Derby Canyon populations.

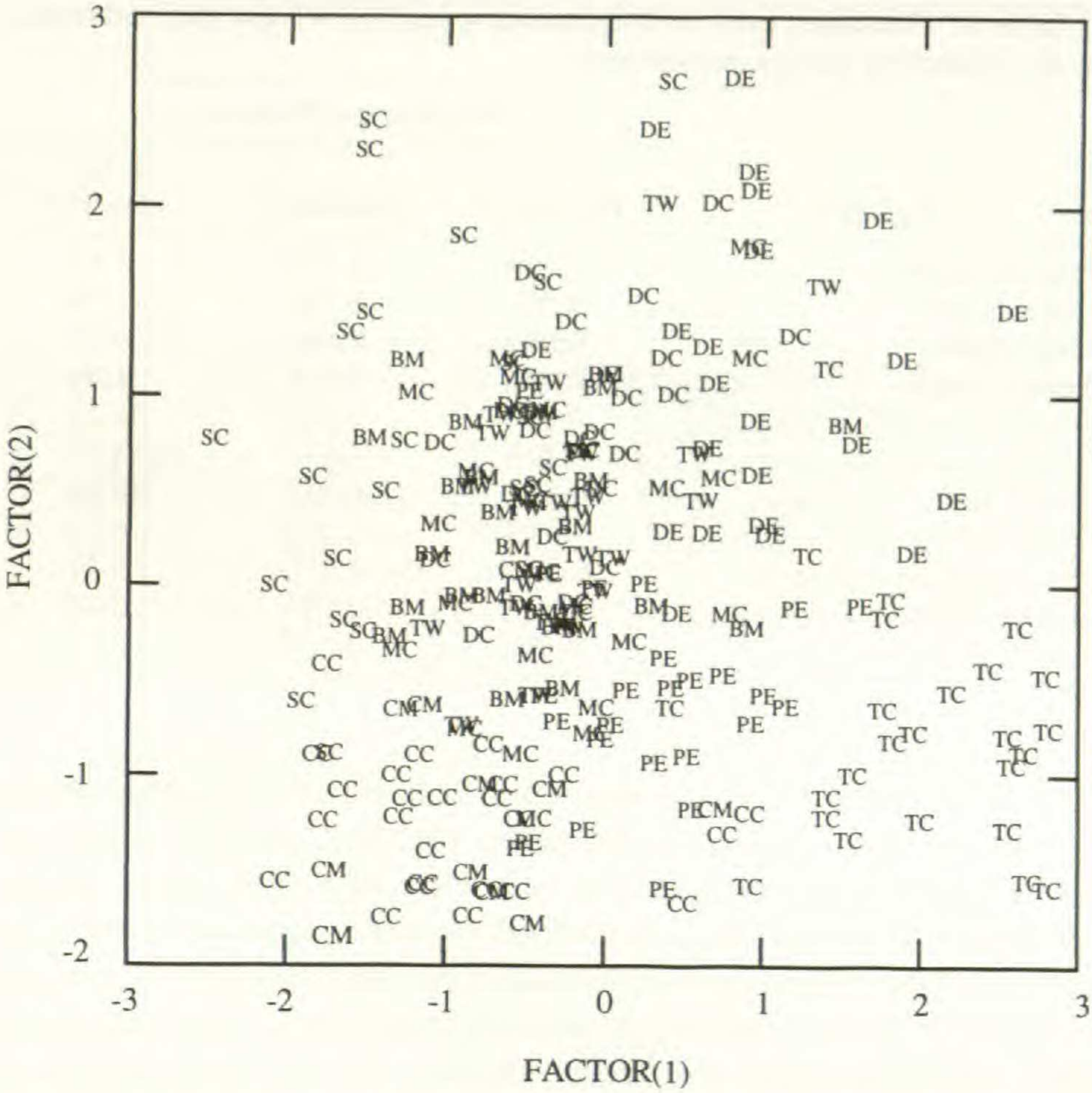

Figure 2. Ordination of populations of *Hackelia* examined in this study based on scores of principal components 1 and 2. The first two components accounted for 56.8% of the total variance (38.5% and 18.3%, respectively). *H. diffusa* var. *arida:* BM = Burch Mountain, TW = Tumwater Canyon; SC = Swakane Canyon, PE = Ponderosa Estates, MC = Moses Coulee, DE = Derby Canyon, DC = Douglas Creek; *H. venusta* (white-flowered form): TC = Tumwater Canyon; *H. venusta* (blue-flowered form): CM = Cashmere Mountain, CC = Crystal Creek.

Discriminant analysis. Table 3 gives the variables used and their relative usefulness in discrimination. The characters that contributed most, in order of importance, were height, fornice appendage height, fornice protuberance length, and limb width. Figure 3 shows the population centroids plotted on the basis of two (out of 9) of the most discriminating functions. Functions 1 and 2 accounted for 85.2% of the ability to distinguish among groups (72.9% and 12.3%, respectively). The total predictability

Table 3. Variables used in discrimination analysis #1 and their usefulness in discrimination among populations.

	Function coefficients (±)		
Variable	Function 1	Function 2	F (to remove)
Pedicel length	0.019	0.158	5.42
Calyx length	0.271	0.189	2.78
Limb width	0.081	0.480	9.37
Anther length	0.016	0.013	1.99
Fornice appendage height	0.604	0.304	34.23
Fornice protuberance length	0.259	0.654	18.45
Plant height	0.659	0.072	48.86
Upper cauline leaf length	0.278	0.264	6.52
Upper cauline leaf width	0.153	0.410	5.71
Lower cauline leaf length	0.163	0.197	5.64
Lower cauline leaf width	0.386	0.228	3.72

that a case from a certain population is correctly classified to that population was 81.0%. Predictability for the Cashmere Mountain and Crystal Creek populations was 82% and 76%, respectively, with individuals not showing affinity to each population grouping with the other. Only two individuals from the Cashmere Mountain population showed affinity to another population (Tumwater Canyon, white-flowered *Hackelia venusta*). Ninety-two percent of cases were correctly classified in the Tumwater Canyon population. Predictability for the *H. diffusa* var. *arida* populations varied from 71% to 96% with deviant individuals grouping with other *H. diffusa* var. *arida* populations. The PCA showed some separation of the Swakane Canyon, Derby Canyon, and Ponderosa Estates populations, which is corroborated to some degree by the discriminate analysis (Figure 3). Predictability for the Swakane, Derby Canyon, and Ponderosa Estates populations was 96%, 83%, and 96%, respectively.

DISCUSSION

Data collected as part of this study indicate that, as currently circumscribed, *Hackelia venusta* comprises two rather discordant elements. The original Tumwater Canyon material is clearly distinct from the high elevation collections which apparently represent an undescribed taxon. We are in the process of completing

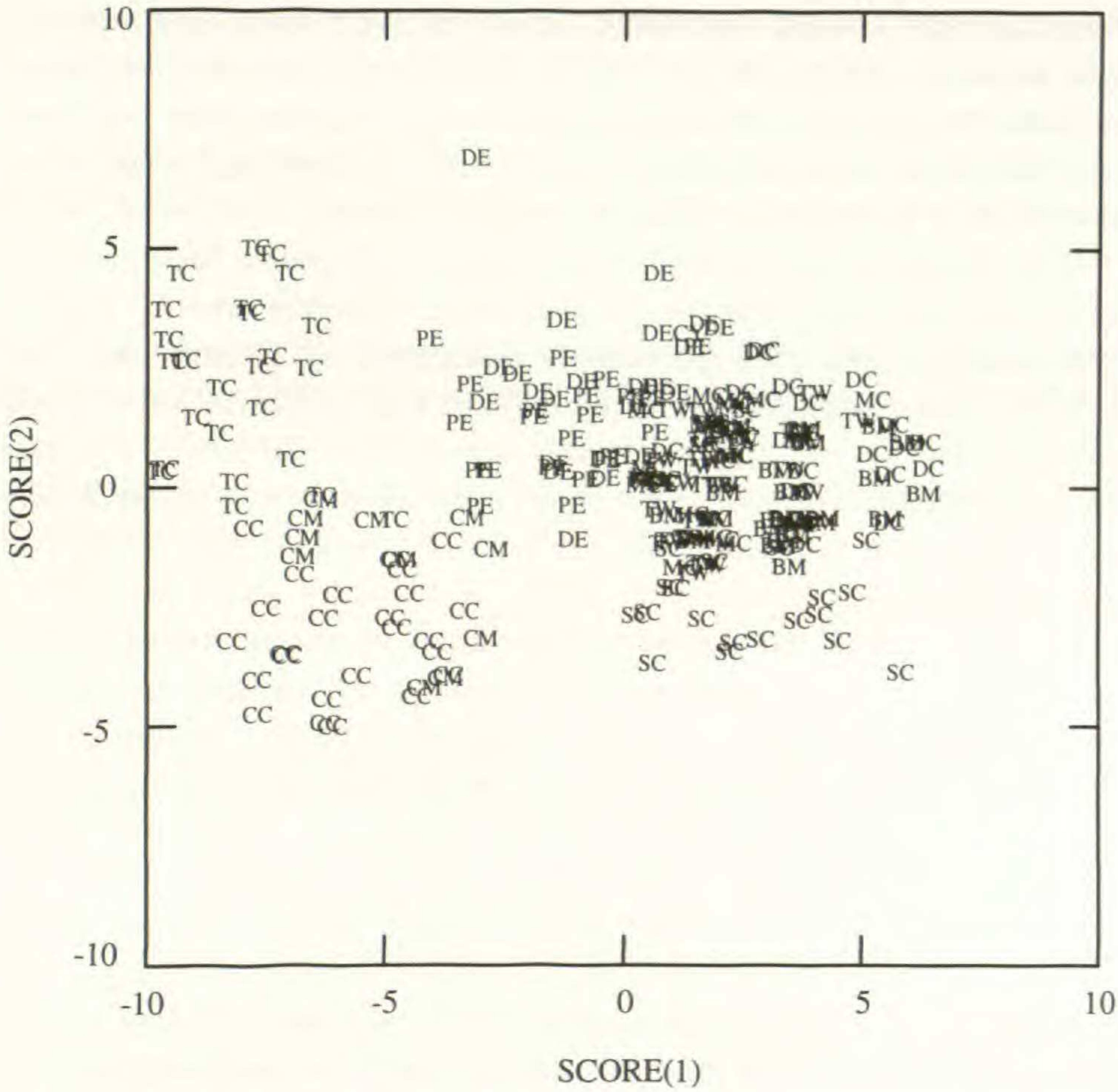

Figure 3. Ordination of populations of *Hackelia* examined in this study based on two most discriminating functions. Functions 1 and 2 accounted for 85.2% of the ability to distinguish among populations (72.9% and 12.3%, respectively). *H. diffusa* var. *arida:* BM = Burch Mountain, TW = Tumwater Canyon; SC = Swakane Canyon, PE = Ponderosa Estates, MC = Moses Coulee, DE = Derby Canyon, DC = Douglas Creek; *H. venusta* (white-flowered form): TC = Tumwater Canyon; *H. venusta* (blue-flowered form): CM = Cashmere Mountain, CC = Crystal Creek.

further studies on these and additional populations. The most obvious morphological distinction between the high elevation and Tumwater Canyon populations is flower color. The high elevation plants are always blue, while the Tumwater Canyon plants are largely white, sometimes with a faint blue tint. This study demonstrates that there are additional morphological distinctions, such as plant height, fornice appendage height, fornice protuberance length, and limb width. The high elevation and Tumwater Canyon populations also occupy markedly different environments, but both occupy similar substrate, scree derived from granodiorite and tonalite (Tabor et al. 1987). Additional factors considered include the absence of intermediate forms between the high and low elevation taxa and plants remain true to form and color when grown in a greenhouse (Harrod unpubl. data).

The results of our study do not suggest allopatric introgression between *Hackelia venusta* in Tumwater Canyon and *H. diffusa* var. *arida* as had been previously suggested by Gentry and Carr (1976). Some populations of *H. diffusa* var. *arida* do have larger flowers, but do not approach the size of the Tumwater Canyon *H. venusta* individuals. Other characters are also dissimilar. However, allopatric introgression between *H. venusta* and *H. diffusa* var. *arida* as posed by Carr (1974) and Gentry and Carr (1976) can not be ruled out by our study since we found considerable variability in floral measurements among *H. diffusa* var. *arida* populations. Three populations (Swakane Canyon, Ponderosa Estates, and Derby Canyon) were separated from each other, but not from other populations of *H. diffusa* var. *arida.* The positions of Ponderosa Estates and Derby Canyon in the PCA and discriminant ordinations were closer to *H. venusta* than any other populations including Swakane Canyon (based largely on floral characteristics). However, it is unclear from our data whether or not gradation in floral characters within populations of *H. diffusa* var. *arida* are the result of allopatric introgression or simply site differences. More information is needed to discover this possible relationship.

Conservation concerns. The Tumwater Canyon *Hackelia venusta* consists of one small population with ca. 150 individuals located near a major state highway. The population in the early 1970s was estimated to occupy a few hundred acres (Carr 1974; Gentry and Carr 1976), but has dramatically decreased due to highway maintenance and habitat loss associated with fire exclusion and subsequent increase in woody vegetation, shading, and stabilization of scree slopes. This population could be lost due to random environmental events and, therefore, is severely threatened. In addition, the high elevation populations are also quite restricted and may be subject to loss from stochastic events. All three populations would benefit from well-developed conservation strategies and subsequent management.

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